COMMONWEALTH INST.
OF ENTOMOLOGY LIBRARY
16 NOV 1958
Eu. 344
SEPARATE

Vol. 110, Part 13, Pp. 363-392 7th November, 1958.

# THE TRANSACTIONS OF THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

*World List* abbreviation: *Trans. R. ent. Soc. Lond.*

## CONTENTS

PAGE

MacLeod, John. The estimation of numbers of mobile insects from low-incidence recapture data . . . . . 363–392,

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.

*Price 11s. 0d.*

# THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

**Founded 1833. Incorporated by Royal Charter 1885.**

**Patron:**
HER MAJESTY THE QUEEN.

## OFFICERS AND COUNCIL FOR THE SESSION, 1958–1959

PROF. O. W. RICHARDS, *President.*
MR. E. B. BRITTON, MR. W. V. HARRIS, DR. H. E. HINTON } *Vice-Presidents.*
DR. N. E. HICKIN, *Treasurer.*
MR. PAUL FREEMAN, *Secretary.*
MR. W. H. POTTS, *Editor.*

*Other Members of Council.*

DR. C. G. BUTLER.
DR. L. G. HIGGINS.
DR. B. M. HOBBY.
MR. T. G. HOWARTH.
DR. J. S. KENNEDY.
DR. A. M. MASSEE, O.B.E.
MR. E. O. PEARSON.
MR. H. L. G. STROYAN.
DR. N. WALOFF.
DR. C. B. WILLIAMS, F.R.S.

MISS E. EVANS, *Registrar.*

*Finance and House Committee.*
MR. H. L. G. STROYAN (Chairman).

DR. J. R. BUSVINE.
DR. C. G. BUTLER.
DR. R. M. GREENSLADE.
DR. A. G. HAMILTON.
MR. A. T. THOMPSON.

*Publication and Library Committee.*
DR. B. M. HOBBY (Chairman).

MR. R. F. BRETHERTON, C.B.
DR. W. J. HALL, C.M.G., M.C.
DR. H. E. HINTON.
MR. T. G. HOWARTH.
MR. H. OLDROYD.

*Committee for the Protection of British Insects.*
MR. H. M. EDELSTEN, O.B.E. (Chairman).

MR. R. B. BENSON.
MR. R. F. BRETHERTON, C.B.
DR. B. M. HOBBY (*and representing the Society for British Entomology*).
CAPT. R. A. JACKSON, C.B.E., R.N.
LIEUT.-COL. W. B. L. MANLEY.
DR. A. M. MASSEE, O.B.E.
DR. N. W. MOORE.
MR. A. ROEBUCK, O.B.E.
MR. N. D. RILEY, C.B.E. (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

## DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society).
   *Mr. N. D. Riley, C.B.E., appointed* 1955.
   *Dr. H. E. Hinton, appointed* 1958.
2. **Local Committee of Management of Wicken Fen.**
   *Mr. H. M. Edelsten, O.B.E.* (nominated by Committee for the Protection of British Insects).
3. **National Trust for Places of Historic Interest or Natural Beauty.**
   *Mr. N. D. Riley, C.B.E., appointed* 1955.
4. **New Forest Association.**
   *Mr. C. W. Mackworth-Praed, appointed* 1948.
5. **New Forest Joint Committee.**
   *Lt.-Col. F. C. Fraser, appointed* 1949.
6. **Field Studies Council.**
   *Dr. W. H. Thorpe, F.R.S., appointed* 1944.
7. **Yorkshire Naturalists' Trust, Ltd.**
   *Dr. W. D. Hincks, appointed* 1946.
8. **The Biological Council.**
   *Dr. N. E. Hickin, appointed* 1952.
9. **The Parliamentary and Scientific Committee.**
   *Dr. N. E. Hickin, appointed* 1953.
10. **British Co-ordinating Committee for Nature Conservation.**
    *Mr. E. B. Britton, appointed* 1954.

# THE ESTIMATION OF NUMBERS OF MOBILE INSECTS FROM LOW-INCIDENCE RECAPTURE DATA

By John MacLeod

(*Ministry of Agriculture (Animal Health Division), (Blackford Field Laboratory, Carlisle)*

E.M.N.

Manuscript received 5th February, 1957

(Read 7th May, 1958)

Contents

| | PAGE |
|---|---|
| I. Introduction | 363 |
| II. Analysis of Methods for Handling Multiple Release and Recapture Data | 365 |
| (1) Development of present-day methods | 365 |
| (2) Relationship of the Fisher, Jackson and Bailey methods | 366 |
| (3) The Jackson recovery estimate | 367 |
| (4) Bailey's method | 368 |
| III. Some Inherent Limitations to the Methods | 369 |
| (1) Effect of mixed populations | 369 |
| (2) Some practical difficulties | 370 |
| IV. A Numerical Example of Serial-release Analysis | 371 |
| (1) The Fisher analysis | 372 |
| (2) The Jackson negative *r* analysis | 375 |
| (3) The Bailey analysis | 378 |
| V. Population Estimates from Pooled Recoveries | 379 |
| (1) Estimation of the loss-rate | 380 |
| (2) Estimates from successive recoveries | 383 |
| (3) Estimate from pooled results | 387 |
| (4) The confidence of the estimate | 388 |
| VI. Discussion | 389 |
| VII. Summary | 391 |
| VIII. References | 391 |

## I. Introduction

The underlying principle of the estimation of population density by marking methods—the Lincoln or Petersen Index—is simply that in a representative sample of a population of which some members have been marked, the ratio of marked to total is an estimate of that ratio in the whole population, and the numerator of the latter ratio is known. The practical application of the index is beset by many difficulties, arising from the dynamic properties of populations and the unavoidable delay between returning marked specimens to the popula-

tion and subsequently sampling it. To gain information on the changes occurring in the marked sample during this interval, extensions of the single release and catch method were introduced. Modifications and improvements of the formula for interpreting the data followed, and manipulative procedures were developed for extracting the additional information. Thus an elaborate background to the method has been built up, to the extent that analysis is now a formidable mathematical exercise. This is well exemplified in a paper by Hammersley (1953), presenting a new method for the analysis of capture-recapture data. An illustrative estimation of the death rate of swifts includes 28 simultaneous equations and, according to the author, took several months to compute, using desk calculators.

Of the methods of handling the data for estimation of numbers, some, *e.g.* those of Leslie and Chitty (1951 *et seq.*) and Craig (1953), are designed for low-density populations, such as small mammals, of which a considerable proportion may be represented by the marked sample, and they depend on appreciable numbers not only of recaptures but of re-recaptures. In many entomological studies the sample will usually be a very small fraction of the total population, the recapture numbers low and the re-recaptures few or *nil*. The recapture data are then quite inadequtae for application of such analytical methods.

There are three main methods generally applicable in insect ecology work. These have been developed in a series of papers by Jackson (1937, 1939, 1940, 1944, 1948), by Fisher and his co-workers (Dowdeswell, Fisher and Ford, 1940, 1949; Fisher and Ford, 1947), and by Bailey (1951 and 1952). The non-statistical argument of Jackson's later method and of Bailey's method is recapitulated in papers by Richards and Waloff (1954) and Richards (1953).

In the estimation of numbers of mobile organisms where the population density is low, or very high, it may prove difficult to obtain adequate data for the application of even these latter analytical methods; they may also be impracticable where specific identification depends on critical study of minute characters, and so precludes immediate release of the captures. Estimates of numbers under such circumstances are often avoided, when in fact they are quite feasible, merely requiring modification and, where an estimate of density only is being sought, some simplification of the usual methods. Unfortunately the present elaborate experimental and analytical procedures are in some danger of being regarded as rituals which must be applied in their entirety to all release-recapture estimations. The point is sometimes overlooked that, for density estimations, the elaborations of the simple Lincoln index are justified only by the need to cover changes in the populations of marked and unmarked specimens in the interim between marking and recapture. If the changes are negligible for this interval or their nature and rate known from independent evidence, then a multiple-phase experiment with complex associated analysis is unnecessary, since it is designed merely to provide estimates of these changes in addition to the density estimate; the formula is unaffected by this ancillary work, and, as in a simple Lincoln index, is completely determined by the three terms—numbers of marked and unmarked specimens caught on the occasion in question and the number of marked specimens available for capture.

In this paper the essential principles underlying the above three methods of analysis of insect data are briefly reviewed, and the elements common to the

three brought out. The special problems of applying the release-recapture technique to blowfly work are used to illustrate some of the difficulties which may be encountered, and a typical set of data on a single blowfly species is examined in turn by each of the methods to illustrate the mechanics of their application.

The examples will also serve to demonstrate the inadequacy of the methods for the type of field material where the recovery incidence is low, and the same set of data is used to examine other possible methods of extracting an estimate under such conditions. Finally, a method is described which has been used (MacLeod and Donnelly, 1957*a*) for the provisional interpretation of experiments on blowfly numbers. This is sufficiently simple and flexible to be applicable to the wide class of problems where more extensive data can be obtained than would be provided by the bare single release and single recovery required for a Lincoln index estimate of density, but where the nature of the problem is such that the classical sequence of serial releases and recoveries is either ruled out or yields data for which the analysis-methods of Fisher, of Jackson and of Bailey are inapplicable.

## II. Analysis of Methods for Handling Multiple Release and Recapture Data

### (1) *Development of Present-day Methods*

In Jackson's earlier work on multiple sampling of tsetse populations (1937, 1939) each release was treated independently. A regular succession of recovery samplings gave information on the change from week to week in the proportion of marked to unmarked flies; from this he obtained by extrapolation an estimate of the recaptures which would be expected to occur if sampling had followed immediately on release instead of a week later. The principle of this method, known as Jackson's positive method, is this. The rate of change of the proportion of marked flies in the population, through dilution, is expected to be regular under normal conditions of population stability, and so the ratio of hypothetical recovery catch at $\text{Week}_0$ after release to the $\text{Week}_1$ recovery, $R_0/R_1$, should be the same as the $\text{Week}_1$ to $\text{Week}_2$ ratio. By reducing his recoveries to a common basis (per cent. of catch) he could thus calculate the extrapolated recovery as $R_0 = R_1^2/R_2$.

This dilution effect arises from two causes—actual loss, through death or departure of the marked flies, and relative loss through birth of unmarked flies. Now, marked and unmarked should have a common loss rate (mortality or migration); a difference in the proportional recovery from two successive releases on a common subsequent occasion should therefore indicate the extent to which change occurred in the first marked group during the period between the two markings, *i.e.* the loss rate, since there is no birth rate. Jackson thus began to consider successive releases in relation to each other. He developed the "negative" method, in which a series of releases is made, followed by a single recovery sampling.

It was an obvious step from there to a combination of the positive and negative methods, *i.e.* serial releases combined with serial recovery samplings. Dowdeswell and his co-workers (1949) used the combination in a study of

Lepidoptera, where, although the interval between markings was almost negligibly short (one day), the investigators desired also to study the nature of any changes occurring in the populations. Jackson, for the same reason and with a one-week interval to allow for, adopted in 1944 a method of analysis involving both his serial releases and recoveries; this he elaborated in detail in 1948. Bailey (1951), suggested his triple-catch method, which is a mathematically acceptable combination of Fisher's and Jackson's method.

### (2) *Relationship of the Fisher, Jackson and Bailey Methods*

The three analysis methods for multiple releases and recoveries—Fisher's, *i.e.* that of Dowdeswell *et al.* (1940), as developed in the paper by Fisher and Ford (1947), Jackson's 1944 method, and Bailey's triple-catch method—will be examined in some detail.

The first two utilise the results of a series of several successive releases; Bailey's triple-catch method relies on two releases and a third catch for recovery only, sacrificing the information from further catches and releases to the requirements of exact tests of significance. At first encounter the three methods appear, at least to the non-mathematically minded, to have little in common, but in fact all three are essentially the application of the Lincoln index principle, *viz.*

$$\text{Population} = \frac{\text{Total marked individuals available}}{\text{Marked individuals recaptured in sample}} \times \text{Total individuals in sample.}$$

The principal difference lies in the method of calculating or expressing the value for available marked individuals and of stating the recoveries value.

In the following discussion the unit of time between catches, which may be any arbitrary period, will for simplicity be called a day.

In Fisher's method the available marked individuals on any given day is calculated simply as the sum-total of survivors from the different releases, assuming a fixed daily percentage loss, and the recapture figure for that day is used directly to estimate the population, at one day after the latest release. The principle of the calculation of loss-rate is most simply explained by an actual example, and is deferred to Section IV.

In Jackson's method, a theoretical percentage recovery on a given day, had there been no loss, is extrapolated from the later observed loss. Two methods are available for this: (*a*) using the subsequent daily percentage losses for two release groups, or (*b*) using the percentage loss for that day, over all release groups. The first he called the negative *r*, since the ratio of the parallel recoveries for each occasion estimates the loss rate; the second, the positive *r* method, gives the ratio of the recoveries for two occasions, *i.e.* estimates the dilution due to birth rate.

Each ratio can be reinforced by similar ratios, of parallel recoveries for subsequent occasions in the case of the $r_-$, and of the two recoveries for the same two days for additional release groups in the case of $r_+$. The relationship of the $r_+$ and $r_-$ ratios to the "positive" and "negative" methods earlier mentioned may seem confusing at first. Thus, the reinforced $r_-$ ratio apparently corresponds to the positive method for a single release, since it uses a succession of recaptures. It is, however, essentially expressing the ratio of

parallel catches, *i.e.* the catches on the same date for two release groups. Conversely the reinforced $r_+$ expresses the ratio of two successive occasions, though including a series of such pairs for the same two dates.

Fisher's estimate of available marked individuals selects from the lattice table of observed data the information, *over all release categories*, for the occasion in question ; Jackson's $r_-$ estimate of recoveries (the better known of his two) is derived from the relationship between successive recoveries from the release group of that day and of the previous day, *i.e.* it selects from the lattice table the recovery information, *over all subsquent days*, relevant to the two releases.

Thus, from the point of view of estimating the population, Fisher's method or Jackson's $r_+$ is usually more appropriate to a series of trapping occasions of which most or all also constitute releases, Jackson's $r_-$ to a limited number of release groups in a long series of trappings.

### (3) *The Jackson Recovery Estimate*

Jackson's method may perhaps most simply be described as follows. Suppose catches are made each day from Monday to Saturday, those up to Friday being marked and immediately released again. The catches are taken at, say, 5 p.m. Let the notation be :

| | Release groups | | | | | |
|---|---|---|---|---|---|---|
| | Mn. | Tu. | W. | Th. | F. | S. |
| Recoveries | | $Mn_1$ | $Tu_1$ | $W_1$ | $Th_1$ | $F_1$ |
| | | | $Mn_2$ | $Tu_2$ | $W_2$ | $Th_2$ |
| | | | | $Mn_3$ | $Tu_3$ | $W_3$ |
| | | | | | $Mn_4$ | $Tu_4$ |

Thus on Thursday 5 p.m. the recaptures consist of :

$W_1$ (the first recaptures of Wed. release), $Tu_2$ (the second recaptures of Tues. release), and $Mn_3$ (the third recaptures of Mon. release).

Assume the day-to-day loss-rate is fixed ; then $W_1 : W_2 : : Tu_2 : Tu_3$ ; equally, if the loss-rate for any single day is constant for all groups $W_1 : Tu_2 : : W_2 : Tu_3$. Jackson's method is based essentially on these relations. $W_0$ is a hypothetical value. It represents the recoveries which would have been obtained from Wednesday 5 p.m. release if the population could have been sampled immediately, *i.e.* at 5 p.m. Wednesday, instead of 24 hours later.

$$W_0/W_1 = Tu_1/Tu_2\ (r_+), \text{ and } W_0/Tu_1 = W_1/Tu_2\ (r_-).$$

If all the recoveries are made comparable, *i.e.* corrected for a sample ($S$) of 100 and a release ($M$) of 100, the theoretical recaptures of $W_0$ can be calculated from a pooled ratio of all paired recaptures from the Wednesday and Tuesday releases :

$$W_0/Tu_1 = \frac{W_1 + W_2 + W_3 \ \ldots}{Tu_2 + Tu_3 + Tu_4 \ \ldots},$$

$$\left(\text{or, by the } r_+ \text{ method, } W_0/W_1 = \frac{Tu_1 + Mn_2 \ \ldots}{Tu_2 + Mn_3 \ \ldots}\right).$$

Since $W_0$ is a percentage $M = 100$, and the population for Wednesday ($P_1 = M\,S/R$) is thus :

$M$ (*i.e.* 100) $\times$ Theoretical sample (*i.e.* 100) divided by $W_0$, or $10^4/W_0$.

### (4) *Bailey's Method*

This triple-catch method is based on a simplification of Fisher's method, but follows Jackson's in using the ratio of recoveries from successive releases to estimate the loss-rate. Let the notation be:

| | | | Recaptures | |
|---|---|---|---|---|
| Day | Sample | Marked | On day 2 | On day 3 |
| 1 | $S_1$ = | $M_1$ | $R_1 1$ | $R_1 2$ |
| 2 | $S_2$ = | $M_2$ | $(R_2 0)$ | $R_2 1$ |
| 3 | $S_3$ | | | |

(Note that the suffix here refers to the day of release. Thus $R_1 1$ and $R_1 2$ are the first and second recaptures from day 1 release.)

The population at day 2 is estimated as

$$P_2 = \frac{S_2 \times \hat{M}_1}{R_1 1},$$

where $\hat{M}_1$ is an estimate of $M_1$ after one day's exposure to loss.

Since the proportional recovery of available specimens from $M_1$ and $M_2$ is assumed to be the same for the same period, $\hat{M}_1 : M_2 :: R_1 2 : R_2 1$, *i.e.* $\hat{M}_1 = M_2 \times R_1 2 / R_2 1$, therefore $P_2 = S_2 \times M_2 / R_1 1 \times R_1 2 / R_2 1$.

The method is quite closely related to that of Jackson, and is in fact foreshadowed in Jackson's 1948 paper. Thus, we could interpret Bailey's formula as an estimate of the population at the beginning of day 2. For this estimate, we would require the available individuals, and an estimate of the sample which would have been caught were $S_3$ taken immediately after release of $M_2$ instead of 24 hours later, and a similar estimate for the imaginary recovery of $M_2$ specimens immediately on release of $M_2$. The available markeds of the day 2 release, at release, is of course the unadjusted $M_2$. Instead of an estimate of what $S_3$ would have been 24 hours earlier, we have an actual catch for that occasion, *viz.* $S_2$. To estimate $R_2 0$—the hypothetical recapture, at release, from the day 2 release—we proceed as before:

$$R_2 0 / R_2 1 = R_1 1 / R_1 2 \text{;} \quad \textit{i.e.}\ R_2 0 = R_1 1 \times R_2 1 / R_1 2.$$

The recoveries in the third catch thus provide a loss-rate ratio with which to estimate the hypothetical extrapolated recovery, $R_2 0$, from the actual day 2 recovery.

The population estimate for day 2, $P = S_2 \times M_2 / R_2 0$, becomes

$$P = S_2 \times M_2 \times R_1 2 / R_1 1 \times R_2 1,$$

which is Bailey's equation.

Since $S_2 = M_2$, the population estimate becomes $S_2^2 / R_1 1 \times R_1 2 / R_2 1$, the second term being the loss-rate ratio provided by the third catch.

It is to be noted that, in so far as the density estimate is concerned, all three methods have the same end-result; each estimate of the population is for one day, from the simple Lincoln-index-type formula: $P = MS/R$ (Lincoln, 1930; Jackson, 1933). It is not suggested that the straightforward Lincoln index is an efficient substitute for the methods. Unlike the Lincoln index, all three methods yield estimates not only of density but of accessions—birth and/or immigration—and of loss-rate. For an estimate of density for a stated

occasion, however, the only advantages of the above methods over the straightforward Lincoln index based on one release and one recapture are (*a*) that they provide some information on the probable loss of marked specimens in the interim between release and sampling, and (*b*) that the serial releases reduce the significance of a large experimental error, possible with a single release, or with a single recovery from a single release.

## III. Some Inherent Limitations to the Methods

Certain implications are accepted in the use of release-recapture data to estimate numbers of any population, *viz.* (1) that the population is indiscriminately sampled, (2) that the marked individuals are not affected by the marking, in respect of their viability or their likelihood of recapture, and become distributed throughout the population from which they were drawn, (3) that the population is either a closed one, or, if emigration and immigration occur, that these are calculable, and (4) that the population is either in balance, *i.e.* the birth-rate plus immigration balances the death-rate plus emigration (and this must also be known if there is an appreciable time-lag in recovery sampling), or, if decreasing or increasing, that the rate of change is known. In insect work, these prerequisites can seldom be realised in their entirety. We shall return to (4) later, in relation to the analysis of an actual set of data. Some of the possibly less obvious implications of (1) merit further discussion at this stage.

### (1) *Effect of Mixed Populations*

A weakness of the release-recapture method is that it takes no account of any component of the population for which there is a *nil* catch for marking. Sometimes the existence of such components may not be known to the investigator. Thus Jackson (1946) found that male tsetse flies were almost completely inactive between their first and second meal; until this inactive component was recognised and allowed for, his estimates of the male population were out by a quite considerable proportion.

A further weakness is that even where a special physiological or other component is recognised and included in the marked sample, a *nil* recapture for it means that no direct estimate can be made of its numbers; *i.e.* the population estimated is not the complete population.

Apart from these inherent defects, the method may give misleading results through misapplication in cases where the population possesses one or more components showing differential behaviour. Consider, for example, blowfly sampling by bait-traps. In this case, where the samples are concentrated from an area of unknown extent in response to attractant baits, the requisite of representativeness assumes a new significance. A bait-trapped sample may fairly be held to be representative of the population at equal risk of capture, but this is unlikely to be the same as the total population, for differences in degree of response to meat-bait are known to exist between species of blowflies and between sexes of a given species, and possibly exist between physiological groups within a sex, *e.g.* in categories of age, hunger, feeding experience and such. A blowfly population is thus a heterogeneous assemblage from the point of view of bait-trap sampling.

A biased representation of the population in the initial sample, in respect of one of those categories which are unchanging, *e.g.* species or sex, is likely to be perpetuated in later samplings by the same technique. The danger in such sampling disproportion is not immediately apparent, and may be insidious with certain categories, *e.g.* size, sex, wariness. For example, if the sexes are sampled for marking disproportionately to their actual numbers because of a tendency to selection of females in the sampling technique, then in the recovery samplings the sexes must be caught in the true proportions in which they occur, *e.g.* through use of a technique of unbiased sampling. If recovery samples have disproportionately few males, *e.g.* through the same sampling technique being used as for the initial catch, the estimate for the species, *i.e.* ignoring sex, will be low. This source of error has been pointed out by Ricker (1948) in relation to fish populations, but has not received attention in other published work.

It should be borne in mind also that if a disproportion in the initial sampling is reversed in the recovery sampling, the estimate will still be biased, but will now be exaggerated. As an actual instance of such reversal (MacLeod and Donnelly, 1957*a*), a laboratory-bred sample of marked *Lucilia caesar* was released into the wild population. The sample happened to have a preponderance of males, but in the subsequent bait-trap samples females occurred to a much greater extent than males, which are relatively indifferent to the attraction of meat-bait. (Where the initial sampling is proportionate, the sex-pooled estimate is true irrespective of sampling bias in the recovery samplings.)

A possible application of these opposing effects may be illustrated by the data for the blowfly *L. sericata* given by Cragg and Hobart (1955). The authors have been careful to give separate male and female estimates, but if the pooled recoveries are used to estimate for the species, an estimate of 22,400 is obtained, as against the authors' 19,300 for the summed sex estimates. The difference in this case is actually less than the sampling error, but suggests the possibility that with more information the pooled results might here give an exaggerated estimate. That would imply that the 1 : 1 sex-ratio of the released group was biased in favour of males and that of the recovery samples in favour of females, or vice versa. The latter is improbable, in view of the observed fact that female blowflies are more attracted to bait-traps than are the males. By varying the sex-ratio of released groups, until the pooled estimate corresponded to the summed sex estimates, the true sex-ratio could be obtained indirectly, as a check on the accuracy of the direct estimates for the separate sexes.

It is doubtful if there are many populations, even of a single organism, which are homogeneous in respect to capture risk. Size differences, difference in agility, in behaviour, *e.g.* between sexes, and so on may well result in disproportionate representation even under sampling conditions generally regarded as reasonably unbiased, such as sweep-net or suction-trap sampling, where no question of differentially operating attractant arises. It seems probable, therefore, that few of the estimates of population which have been made can be regarded as completely free of bias; in the majority of cases the bias will be towards under-estimation.

(2) *Some Practical Difficulties*

In the case of a species complex, such as blowflies, it will obviously be of little value to estimate the total population, treating all the species in wild-

caught samples as a single category. The alternative, of estimating separately for each species component, will usually mean inadequately low releases for the less frequent species (*e.g.* see Table VI). The field worker will therefore be faced with the choice of concentrating on one species at a time in order to get reasonable numbers, or of using laboratory-bred material. Both courses are open to objection, the first on the grounds that in a study of the interrelations of a group of species, the results so obtained lose precise comparative value, the second because laboratory-bred material cannot be assumed to be representative of the wild population to which it is added. This latter objection is discussed in detail elsewhere (MacLeod and Donnelly, 1956).

In experiments where the recoveries are expected to be relatively few, as in blowfly work, there is this major difficulty in applying the serial release methods: since mass-marking does not allow of re-marking and release of recaptures (MacLeod and Donnelly, 1957*b*), individual handmarking is required. This has two objections. First, the mortality incident on identifying and marking the catch is high, and the proportion of the population caught may thus be considerably greater than the proportion marked and released. The discrepancy may introduce an error, which is cumulative, for each release containing earlier marks. If the loss of marked specimens is serious, it will of course invalidate the theory of the population estimate from serial release-recaptures.

The second objection arises from the fact that individual handmarking is time-consuming, and so limits the numbers which can be used. Where, as is generally the case, the recovery incidence is low, there may thus be many sampling days with *nil* recaptures, even of the latest release. A *nil* first recovery for a given day, *e.g.* $R_1 1$, means that Jackson's extrapolated recovery for the following day, ($R_2 0$), cannot be calculated by his 1944 ($r_-$ or $r_+$) method. Further, since recoveries of earlier releases than the last tend to be increasingly infrequent, either formula for the recovery estimate will sometimes contain the first three observation terms only, *viz.*:

$$R_2 0 = \frac{R_1 1 \times R_2 1}{R_1 2}.$$

In such cases no estimate for $R_2 0$ will be possible by Jackson's 1944 method if any one of the three recoveries is *nil*. In fact the method, or Bailey's triple-catch modification, is only suitable for relatively high incidence of recaptures.

Fisher's method allows of estimates of density for all days except those on which *nil* recoveries occurred, but if there are many such it becomes increasingly difficult, as shown in the following worked example, to decide on the appropriate loss-rate to be used in the calculation of the number available each day.

## IV. A Numerical Example of Serial-release Analysis

As an actual example of the application of the three analysis methods discussed above, and also to illustrate some of the possible objections when these methods are applied to certain types of insect data, certain release-recapture experiments on blowflies with successive releases (MacLeod and Donnelly, 1957*a*) may be used. In these, the highest recovery was for the

"Lab. Section" test area of experiment $R/R_2$, and the figures for the predominant species, *Calliphora erythrocephala* (females only), for this test are thus the most promising data on which to try the analysis methods.

### (1) *The Fisher Analysis*

In the arithmetical manipulations I have adopted a different procedure from that given by Fisher and Ford (1947), and this perhaps calls for some explanation. A disadvantage of their method is that the loss-rate to be used is decided on by a process of trial-and-error repetition of the calculations involved. These are at best laborious, and for certain purposes are unnecessarily cumbersome and inconvenient. Thus, the tabulated numbers of available insects each day are calculated in relation to a predetermined final date, and

TABLE I.—*Data for* C. erythrocephala ♀♀. *Expt.* $R/R_2$: *Lab. Section.*

| Date | *A* sample | *B* (Recaptures) | *C* (Recaptures) | *D* | *E* | *F* | *G* | *H* |
|---|---|---|---|---|---|---|---|---|
| 11.ix . | 77 | . | | 62 | . | . | . | . |
| 12.ix . | 46 | . | | 55·80 | **23** | . | . | . |
| | | | | 55·8 | . | . | . | . |
| 13.ix . | 314 | . | | 50·22 | 20·70 | **241** | . | . |
| | | | | 100·4 | 20·7 | . | . | . |
| 14.ix . | 27 | . | | 45·20 | 18·63 | 216·90 | . | . |
| | | | | 135·6 | 37·3 | 216·9 | . | . |
| 15.ix . | 668 | 2 | . | 40·68 | 16·77 | (2) 195·21 | . | . |
| | | | | 162·7 | 50·3 | 390·4 | . | . |
| 16.ix . | 167 | 1 | 2 | 36·61 | 15·09 | (1) 175·69 | . | . |
| | | | | 183·1 | 60·4 | 521·1 | . | . |
| 17.ix . | 242 | 3 | 3 | 32·95 | 13·58 | (3) 158·12 | **220** | . |
| | | | | 197·7 | 67·9 | 620·5 | . | . |
| 18.ix . | 187 | 1 | 6 | 29·66 | 12·22 | 142·31 | (1) 198·00 | . |
| | | | | 207·6 | 73·3 | 681·6 | 198·0 | . |
| 19.ix . | 142 | . | 7 | 26·69 | 10·99 | 128·08 | 178·20 | **96** |
| | | | | 213.5 | 76·9 | 732·5 | 354·4 | . |
| 20.ix . | 1,194 | 11 | 7 | 24·02 | 9·89 | (2) 115·27 | (7) 160·38 | (2) 86·40 |
| | | | | 216·2 | 79·1 | 764·9 | 478·1 | 86·4 |
| 21.ix . | 816 | 7 | 18 | (1) 21·62 | 8·90 | (2) 103·74 | (2) 144·34 | (2) 77·76 |
| | | | | 216·2 | 80·1 | 765·9 | 545·4 | 151·5 |
| 22.ix . | 432 | 3 | 25 | 19·46 | (1) 8·01 | (1) 93·37 | (1) 129·91 | 69·98 |
| | | | | 203·1 | 80·1 | 750·3 | 599·6 | 197·9 |
| 23.ix . | 196 | 1 | 28 | (1) 17·51 | 7·21 | 84·03 | 116·98 | 62·98 |
| | | | | 198·1 | 68·3 | 731.0 | 635·5 | 235·9 |
| 24.ix . | 557 | 5 | 29 | 15·76 | 6·49 | (2) 75·63 | (1) 105·23 | (2) 56·68 |
| | | | | 178.9 | 65·9 | 710·9 | 659·6 | 263·4 |
| 25.ix . | 432 | . | 34 | 14·18 | 5·84 | 68·07 | 94·71 | 51·01 |
| | | | | 170·5 | 62·9 | 660·8 | 661·7 | 270·1 |
| 26.ix . | 578 | 4 | 34 | 12·76 | 5·26 | (2) 61·26 | (2) 85·24 | 45·91 |
| | | | | 161·4 | 59·6 | 627·4 | 659·2 | 279·4 |
| 27.ix . | 936 | 4 | 38 | 11·48 | 4·73 | (2) 55·13 | (2) 76·72 | 41·35 |
| | | | | 151·7 | 55·9 | 561·8 | 627·2 | 282·6 |
| 28.ix . | 534 | . | 42 | 10·33 | 4·26 | 49·62 | 69·05 | 37·19 |
| | | | | 141·6 | 52·2 | 489·3 | 583·6 | 280·7 |

those available on an intermediate day must be subsequently calculated from the tabulation. Yet, in experiments where only a limited number of trappings for release are made, followed by a series of purely recovery trappings, this series may be continued until hope of further recoveries is abandoned. In such case, it is obviously more convenient to calculate the total availables for each successive day directly. The effective end-date may then be decided at will as the analysis progresses. Further, by this "progressive" method of manipulation the numbers available on any intermediate day can be read off directly from the table.

In this method, as in Jackson's method next illustrated, a recovered insect might have two or more marks, and would then be recorded as two or more recoveries.

*Calculations modified from Fisher and Ford*

| $K$ (Survivors) | $K-C$ (Available) | Estimate | $L$ ($E.F.D$) | $M$ ($L/K-C$) | Survival in fly-days: Act. | Survival in fly-days: Exp. ($M \times B$) | Survival in fly-days: Discrepancy |
|---|---|---|---|---|---|---|---|
| 55·8 | 55·8 | | 55·8 | 1·00 | | | |
| 70·92 | 70·92 | | 121·1 | 1·71 | | | |
| 280·73 | 280·73 | | 389.8 | 1·39 | | | |
| 252·66 | 252·66 | 56,343.2 | 603·4 | 2·39 | 4 | 4·78 | +0·78 |
| 227·39 | 225·39 | 18,932.8 | 764·6 | 3·39 | 3 | 3·39 | +0·39 |
| 204·65 | 201·65 | 12,250·2 | 886·1 | 4·39 | 12 | 13·17 | +1·17 |
| 382·19 | 376·19 | 35,361·9 | 1,160·5 | 3·08 | 1 | 3·08 | +2·08 |
| 343·96 | 336·96 | | 1,377·3 | 4·09 | | | |
| 395·96 | 388·96 | 38,733·9 | 1,624·7 | 4·18 | 37 | 45·98 | +8·98 |
| 356·36 | 338·36 | 34,555·0 | 1,759·1 | 5·20 | 38 | 36·40 | −1·60 |
| 320·73 | 295·73 | 32,012·8 | 1,831·0 | 6·19 | 24 | 18·57 | −5·43 |
| 288·71 | 260·71 | 25,679·9 | 1,868·8 | 7·17 | 12 | 7·17 | −4·38 |
| 259·79 | 230·79 | 21,463·5 | 1,878·7 | 8·14 | 39 | 40·70 | +1·70 |
| 233·81 | 199·81 | | 1,826·0 | 9·14 | | | |
| 210·43 | 176·43 | 20,430·6 | 1,786·5 | 10·13 | 44 | 40·52 | −3·48 |
| 189.38 | 151·38 | 28,368·6 | 1,677·2 | 11·09 | 48 | 44·36 | −3·64 |
| 170·45 | 128·45 | | 1,547·4 | 12·05 | | | |

The calculations are given in Table I. This table is in effect a lattice table, containing the usual information on samples, releases and recoveries, laid out as in the trellis diagram with the recoveries per release and per day in rows at right angles to each other. Included in the lattice part, however, are the calculated survivors, and their cumulative flying days. The remainder of the calculations are after the pattern given by Fisher and Ford except that allowance has been made for captured specimens, which in our experiments were not released again, and for which the standard manipulations make no allowance.

For purposes of exposition the table includes more columns than would ordinarily be required, *e.g.* the recovery figures are given thrice. Column *A* is the wild sample trapped, and opposite the same date is given the number of these which were marked and released on the five release days (Columns *D* to *H*, heavy type), and the recaptures found in the sample (Column *B*, from all releases, and bracketed figures in columns *D* to *H*, from the individual releases).

For each date in columns *D* to *H* there are two calculated figures. The upper is the theoretical survivors, calculated as a geometric series (decreasing by a fixed percent., *e.g.*, 10 per cent.). The total for these for each day is given in column *K*. From the theoretical survivors we must deduct all non-released captures up to the preceding day (column *C*). The remainder $(K - C)$, represent the available marked, *i.e.* those at risk of capture on that day. For the population estimate Bailey's correction for low recovery rate,

$$\frac{(K - C)(A + 1)}{B + 1}$$

instead of $(K - C)A/B$, has been used.

The lower figure in columns *D* to *H* is the total fly-days which can be credited to those flies still available. It is obtained by multiplying the upper figure, less cumulative recaptures of that release up to the previous day, by the number of days since release. The summation of these effective fly-days ($E.F.D$, column *L*), for any given day divided by the total available $(K - C)$ on that day gives the average survival-since-release of the available marked flies (column *M*). If the number of recaptures on any day is multiplied by the average age-since-release of the marked population on that day we have a theoretical total of days survived—the " expected survival ", in fly days—for that group of recaptures.

Table I survivals are calculated on a 90 per cent. basis. The discrepancies between expected and actual survival are listed in Table II for survival rates of 95 per cent. to 75 per cent. The aggregate discrepancy for 90 per cent. is the lowest, but it is clear from the table that with none of the rates is the discrepancy randomly distributed in time ; the early loss rate was greater than 25 per cent. (*i.e.* even 75 per cent. survival gives a positive discrepancy), but within a day or two after all the releases were completed the rate was less than 5 per cent. This is in accord with other evidence of the dispersal pattern for a concentration of blowflies (*see later*).

Apart from the inapplicability of a constant loss-rate to the present data, it is clear that the Fisher analysis method, as conventionally applied, would also be unsuitable for estimating blowfly population changes because of the discrepancies between numbers caught and released, which are likely to include

a proportion of the recaptures. These discrepancies are due to deaths in the traps, and to handling loss, the proportion of the catch represented by this latter tending to increase with the numbers. They are thus to a large extent an inescapable feature of blowfly recapture data.

There is no simple method of estimating the error of population estimates obtained by Fisher's method.

TABLE II.—*Survival discrepancies for different survival factors*

| | | Discrepancy between expected and actual survival | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 0·95 | | 0·90 | | 0·85 | | 0·80 | | 0·75 | |
| Date | Actual survival | + | − | + | − | + | − | + | − | + | − |
| 15.ix . | 4 | 0·84 | . | 0·78 | . | 0·72 | . | 0·66 | . | 0·6 | . |
| 16.ix . | 3 | 0·43 | . | 0·39 | . | 0·36 | . | 0·33 | . | 0·3 | . |
| 17.ix . | 12 | 1·29 | . | 1·17 | . | 1·08 | . | 0·99 | . | 0·93 | . |
| 18.ix . | 1 | 2·37 | . | 2·08 | . | 1·79 | . | 1·49 | . | 1·20 | . |
| 20.ix . | 37 | 13·27 | . | 8·98 | . | 4·58 | . | 0·18 | . | . | 4·0 |
| 21.ix . | 38 | 1·2 | . | . | 1·6 | . | 4·57 | . | 7·48 | . | 10·49 |
| 22.ix . | 24 | . | 4·2 | . | 5·43 | . | 6·75 | . | 8·19 | . | 9·81 |
| 23.ix . | 12 | . | 4·4 | . | 4·83 | . | 5·31 | . | 5·87 | . | 6·63 |
| 24.ix . | 39 | 3·85 | . | 1·7 | . | . | 0·85 | . | 4·35 | . | 10·35 |
| 26.ix . | 44 | . | 1·6 | . | 3·48 | . | 6·0 | . | 11·24 | . | 98·84 |
| 27.ix . | 48 | . | 1·72 | . | 3·64 | . | 6·76 | . | 18·88 | 14·68 | . |
| Net discrepancy | | +11·33 | | −3·88 | | −21·71 | | −52·36 | | −122·4 | |

(2) *The Jackson Negative r Analysis*

In Table III the same recaptures have been expressed as a double percentage. If $A$ recaptures occur in a sample of $B$ flies, and the release group contained $C$ flies, then $100\ A/B \times 100/C$ should occur in a sample of 100, for a release group of 100. Each recapture value is therefore multiplied by $100^2/BC$.

A *nil* recovery on the second day for the release of 11.viii corresponding to the hypothetical day$^0$ recovery for 13.viii, ($R_{13}0$), makes an estimate of the latter impossible. Similarly the extrapolated recovery $R_{19}0$ corresponds to the *nil* recovery $R_{17}2$, and cannot be calculated.

The corresponding day for day 0 of the 17.viii release is day 4 of 13.viii, *i.e.*

$$\frac{R_{17}0}{R_{13}4} = \frac{R_{17}1 + R_{17}2 \quad \ldots}{R_{13}5 + R_{13}6 \quad \ldots}$$

$$R_{17}0 = 0{\cdot}5144 \times \frac{\begin{array}{r}0{\cdot}2431 + 0 + 0{\cdot}2665 + 0{\cdot}1114 + 0{\cdot}1052 \\ + 0 + 0{\cdot}0816 + 0 + 0{\cdot}1572 + 0{\cdot}0971\end{array}}{\begin{array}{r}0 + 0 + 0{\cdot}0695 + 0{\cdot}1017 + 0{\cdot}0961 \\ + 0 + 0{\cdot}1490 + 0 + 0{\cdot}1436 + 0{\cdot}8870\end{array}}$$

$$= 0{\cdot}8423.$$

The population estimate for 17.viii, *i.e.* $10^4/0{\cdot}8423 = 11{,}872$.

TABLE III.—*Table I data expressed as Jackson's corrected recoveries*

| | Samples | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 46 | 314 | 27 | 668 | 167 | 242 | 187 | 142 | 1194 | 816 | 432 | 196 | 557 | 432 | 578 | 936 |
| 11.viii | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27.viii |
| 62 | . | . | . | . | . | . | . | . | . | 0·1977 (1) | . | 0·8229 (1) | . | . | . | . |
| | 23 | . | . | . | . | . | . | . | . | . | 0·1006 (1) | . | . | . | . | . |
| | | 241 | . | 0·1242 (2) | 0·2485 (1) | 0·5144 (3) | . | . | 0·0695 (2) | 0·1017 (2) | 0·0961 (1) | . | 0·1490 (2) | . | 0·1436 (2) | 0·887 (2) |
| | | | | | | 220 | 0·2431 (1) | . | 0·2665 (7) | 0·1114 (2) | 0·1052 (1) | . | 0·0816 (1) | . | 0·1572 (2) | 0·971 (2) |
| | | | | | | | | 96 | 0·1744 (2) | 0·2553 (2) | . | . | 0·3740 (2) | . | . | . |

It is obvious from the absence of any trend of change in the daily proportions of recaptures from each release, or for each day over successive releases, that they are not adequately reflecting changes in the ratio of marked to unmarked, owing to emergences replenishing one lot and not the other ; nor are they reflecting differences in relative numbers of survivors from successive releases, owing to their exposure for different periods to an unreplaced loss. This failure is presumably because of the low incidence of recoveries, with frequent *nil* days.

For those interested in the further information to be obtained from the Jackson analysis, the death-rate, emergence rate, and the variance are calculated as follows :

The death rate over the period 18–19.viii is given by the difference in relative numbers between the parallel recoveries $R_{19}1$ and $R_{17}3$, expressed as a fraction of $R_{19}1$, *i.e.*

$$\frac{R_{19}1 - R_{17}3}{R_{19}1},$$

*or*

$$1 - \frac{R_{17}3}{R_{19}1}.$$

The ratio $R_{17}3/R_{19}1$ is Jackson's $r_-$, or the survival rate. Reinforced by later parallel recoveries, it becomes

$$\frac{R_{17}3 + R_{17}4 + R_{17}5 + R_{17}7}{R_{19}1 + R_{19}2 + R_{19}3 + R_{19}5},$$

*or* 0·7, *i.e.* the death rate over the two days is 0·3, or 15 per cent. per day. Estimated from the parallel recoveries for the 13.viii and 17.viii releases, for the six occasions between 20.viii and 27.viii, $r_-$ is 0·8. That is, the death rate estimate on 17.viii, *viz.*, 0·2 for four days, is only a third of the above, or 5 per cent. per day (0·26 for four days if estimated from the same days as for the 19.viii estimate).

The emergence rate is estimated from the difference in relative recovery on two successive occasions. Thus emergence between 20.viii and 21.viii will decrease the proportional recovery on 21.viii. The decrease expressed as a fraction of the 20.viii recovery is for the 17.viii release

$$\frac{R_{17}3 - R_{17}4}{R_{17}3},$$

or

$$1 - \frac{R_{17}4}{R_{17}3}.$$

The $r_+$ fraction

$$\frac{R_{17}4}{R_{17}3}$$

may be reinforced by the recoveries on these two days from the release of 13.viii, *i.e.*

$$r_+ = \frac{0{\cdot}1114 + 0{\cdot}1017}{0{\cdot}2665 + 0{\cdot}0695} = 0{\cdot}63.$$

The emergence rate $(1 - r_+) = 0{\cdot}37$. The rate, calculated for these two days for the 13.viii release, is

$$1 - \frac{0{\cdot}1017}{0{\cdot}0695},$$

*i.e.* a minus quantity ! The emergence rate, again for 20–21.viii, calculated on the reinforced $r_+$ ratio for the 19.viii release, is 1 — 0·92, or 0·08. Thus, of the three estimates of

emergence rate per fly on 21.viii, based on the same two successive days, two differ by as much as four times; the third is a qualitatively different minus estimate, *i.e.* should indicate immigration of marked flies!

The variance of the $r_-$ and $r_+$ estimates is given by Jackson as

$$\frac{r + r^2}{R_a + R_b} \quad \ldots$$

where $R_a + R_b$ . . . are the actual recoveries (*i.e.* not expressed as a double percentage), corresponding to the percentage values used in calculating the denominator of the $r$ fraction. For the different estimates of $r$ calculated above, the variances are:

| | | | | |
|---|---|---|---|---|
| $r_-$ | 17/19 | (0·7) | $V = 0·2$ | S.E. 0·45 |
| | 13/17 (1) | (0·8) | 0·196 | 0·3 |
| | (2) | (0·74) | 0·117 | 0·34 |
| $r_+$ | 20/21 (1) | (0·63) | 0·114 | 0·34 |
| | (2) | (0·92) | 0·16 | 0·4 |

*i.e.* the $r$ estimates themselves are only about twice their standard errors. The high variance is due to the low incidence of recoveries.

A significant increase of $r_-$ over $r_+$ for any given interval means that the population has increased, and conversely a higher $r_+$ means a decrease. It is obvious, however, that the use of the $r$ index is not reliable for the type of recapture data represented by this example.

### (3) *The Bailey Analysis*

In this method the second mark in the case of a re-recapture is ignored, all recaptures being recorded only against the date of first marking. The arithmetical procedure may be illustrated by adapting the data of Table I. Suppose only the three catches, 13.viii, 17.viii and 21.viii, were made, *i.e.* that the trapping interval was four days.

The recoveries are:

ex 13.viii, 3 on 17.viii, 2 on 21.viii.
ex 17.viii, " 2 on 21.viii.

The basic formula for the estimate on 17.viii:

$$\frac{(\text{Sample})^2 \times R_{13}2}{R_{13}1 \times R_{17}1}$$

is modified for low recoveries:

$$\frac{(\text{Sample})(\text{Sample} + 1)(R_{13}2)}{(R_{13}1 + 1)(R_{17}1 + 1)}.$$

(Since the marked group on 17.viii is appreciably less than the sample, the actual number marked instead of the sample is used for the first term.)

$$\frac{220 \times 243 \times 2}{4 \times 3} = 8910. \quad . \quad . \quad \text{(Estimate 1)}$$

If the intervening catches be included by regarding the catches as fractionated samplings, the total sample on 17.viii is :

$$27 + 668 + 167 + 242 = 1104, \text{ and the recovery } 6.$$

The recoveries on 21.viii are : for 13.viii, 4 ; for 17.viii, 10. The estimate is

$$\frac{1104 \times 243 \times 4}{7 \times 11} = 13{,}936 \quad . \quad . \quad \text{(Estimate 2)}$$

Estimate 2 is almost as much above the Jackson estimate (11,900) as estimate 1 is below it. In any case the gross discrepancy between marked and total sample size in estimate 2 makes its validity questionable.

Bailey's formula for an estimate of the variance where the recoveries are low is :

$$V = (\hat{P}_2) - \frac{S_2{}^2 (S_2 - 1)(S_2 + 1) R_1 2 (R_1 2 - 1)}{(R_1 1 + 1)(R_1 1 + 2)(R_2 1 + 1)(R_2 1 + 2)}.$$

The variance of estimate 1 is $7720^2$. This is so high, on account of the low recovery values, that the estimate is practically worthless.

The rate of decrease of the population from 13.viii to 17.viii is estimated from the ratio of the 21.viii recoveries from these two releases (Table III) : $2/220 \times$ decrease fraction $= 2/241$, *i.e.* fraction $= 440/482, = 92/100$, or 2 per cent. per day.

The rate of increase is indicated by the difference in the recovery rate for the 13.viii marked group on the two successive occasions, 17.viii and 21.viii : recovery rate for 13.viii on 21.viii, multiplied by the population increase factor, equals recovery rate for 13.viii on 17.viii. $2/816 \times$ Factor $= 3/242$, *i.e.* the population has increased fivefold sometime between 17.viii and 21.viii.

Examination of Table I shows that there was, in fact, an approximately five-fold increase in sample size about this time. There is no corresponding increase in the recaptures from the 13.viii release, as would be expected if this increase were an activity effect, though the recaptures for the 17.viii release show a sharp peak on 20.viii. Although there is reason to believe that the population of *C. erythrocephala* on the Lab. section underwent a sudden increase at this time (MacLeod and Donnelly, 1957*a*), it is nevertheless obvious that no inference of the extent of population change is permissible merely from the evidence of the above Bailey analysis, in view of the difference which one extra fly would have made to the estimate of the increase factor.

## V. Population Estimates from Pooled Recoveries

The principal reason for serial release as against single release is to supply reliable information on population changes. But, as has been shown, if the recovery incidence is low, serial release methods may fail to do this. In blowfly work, serial release implies incomplete identification of some of the species in the samples. The " single release " method was therefore adopted as standard in later experiments. The sample to be marked and released is identified to species where this can be done without difficulty ; those species difficult to

separate without detailed examination, *e.g.* the *Lucilia caesar* group (*L. caesar*, *L. illustris* and *L. ampullacea*) and the *Acrophaga-Calliphora* intermediate types (*A. subalpina*, *C. uralensis*, *C. loewi*), are identified merely to the group. The proportions of the species forming these groups, in the released sample, are later estimated either from a representative subsample retained from the marking catch, if this is adequately large, or by interpolation from a sample taken for identification the day before marking and the first recovery sample, the day after. This initial sample and the serial recovery samples are killed for identification. An advantage of this method of single release plus serial recovery sampling is that the daily catch may be stored for later examination. The catch may thus be increased to the limit of trapping resources to increase the recapture incidence where the likelihood is low; this is impossible where the sample must be immediately identified, as in serial release.

It was obvious, however, that the objections to Jackson's $r$ estimate discussed earlier would apply with even greater force to his pre-1944 method of estimating loss-rate from a single release, so it was decided to assess loss-rate independently of the experiment. The series of successive recovery samplings was retained, so as to obtain some kind of "average population" estimate, in view of the expected high frequencies of poor- or *nil*-recovery days.

The method of single release followed by serial recovery, with loss-rate estimated independently of the internal evidence of the experiment, has been successfully exploited by Gilmour, Waterhouse and McIntyre (1946) in their study of population numbers of *L. cuprina* in Australia. In this work the expected rate of decrease in the number of marked flies remaining in the trapped area was calculated from a synthesis of laboratory evidence on death-rate and of theoretical expectation of spread on the assumption of random movement of the liberated flies.

### (1) *Estimation of the Loss-rate*

It is well to consider for a moment the implications of an "average population" estimate, and of the estimate of loss-rate as applied to a large group of blowflies released at a single point, around which a limited area is to be sampled subsequently.

A succession of recovery samplings will provide a series of Lincoln index estimates of the population density for successive days. These will show fluctuation. To the extent that the variations represent sampling error of the estimate some sort of average value must be struck. Equally, in so far as they represent true population fluctuations, it would obviously be of little descriptive value to cite any one estimate of density unless this were representative of the group of estimates among which it occurred, *i.e.* an average.

Since the population level may well alter markedly in quite a short period, this average estimate should be over a period of not more than a few days. During this period, the available flies will be subject to loss from two causes, (*a*) mortality, which includes "normal" death from old age and "wastage", death from accident and/or adverse environment, and (*b*) emigration beyond the zone of influence of the traps. Where the trapped area is restricted to a few hundred yards, it is not to be expected, *a priori*, that the loss-rate from all

causes will be constant for a run of days, as assumed in the Fisher analysis, *i.e.* that both emigration and death-rate will be exponential. They must therefore be considered separately.

It is possible to assign a value for mortality from the observed death-rate of a confined group of similar flies, plus an arbitrary allowance for wastage. The "physiological" mortality, at least in cage colonies, is apparently an arithmetic rather than a geometric series, the rate increasing with time; the wastage mortality will presumably be mainly in geometric series—a function of density.

The dispersal of a concentration of blowflies from the primary focus appears on the other hand to be explosively abrupt in comparison with their subsequent emigration out of the area. A somewhat similar effect was reported for tsetse flies (Jackson, 1939), the males travelling 0·4 miles outwards in the first week, as against an average of only one mile over six weeks. In a preliminary experiment on dispersal at this laboratory the distribution of released flies, within the first week, was apparently represented more closely by a density varying inversely with the distance than with its square; the greater part of this redistribution apparently occurred within the first two days.

Cragg and Hobart (*loc. cit.*) obtained a reasonably constant loss-rate with serially released *L. caesar* (chemical bait-trap data) but, as the authors point out, the conditions at the site of release and capture were atypical, and apparently induced a high and maintained local concentration of the species.

The chemical bait traps were confined to the release area. From their results with more widely distributed meat traps, the authors calculated the distribution of their marked flies, on the basis of a uniformly distributed general population. From the figures given, it appears that the number of marked flies per trap at one-eighth and one-quarter mile distance were equal, and the number at one-half mile one-third of that at a quarter mile. This means that the number which had moved out for at least a quarter mile was greater than that still within one-eighth mile of the release point, and that the ratio of marked flies at a quarter mile to those at a half mile was only 1·5 to 1. The recoveries on which these figures are based apparently occurred mainly within the first week of release, indicating once more a non-random rate of initial spread of a concentration of released flies.

It would thus seem advisable to follow the Australian workers in allowing for emigration-loss separately, instead of including it with the mortality rate in an assigned geometric or arithmetic decrease progression.

Samples of wild-caught flies, retained in the laboratory as longevity checks for the released groups, gave survival curves which were nearer to linear than exponential regressions of numbers on time, with the 50 per cent. point near the middle of the curve, though the curves tended to show accelerated mortality towards the end. The 50 per cent. level was reached in about four weeks in the summer experiments, and in a fortnight to three weeks in late autumn. On this basis, a mortality rate of 2 per cent. in summer and 4 per cent. in autumn was used for calculating survival of released groups.

For calculating dispersal rate, some unit of territory for random fly-movement is required. From general observation a reasonable estimate of the linear displacement due to a single random flight would appear to be between 50 and 100 yards. After the second of two standard-length flights, the fly in

50 per cent. of cases will be still within a square centred on the starting point and with a side equal to two flight-lengths. If the average displacement for one flight is taken as 75 yards, these " 50 per cent. squares " after two flights, for all possible direction of the first flight, are contained in a circle of which the radius is $\sqrt{2} \times 75^2$, or approximately 100 yards. The unit is therefore taken provisionally as a circle of 100 yards radius.

As previously mentioned, a concentration of released flies was found to have dispersed, during the first few days, to a greater extent than would be represented by a distribution varying inversely with the square of the distance. Pending more precise investigation of the dispersal pattern, it is convenient, however, to consider the dispersal by the middle of the first week as conforming to the inverse square relation.

In a series of concentric circles, of which the first has radius half a diameter of " unit territory ", and each successive radius increases by one diameter, the areas of the successive zones (annuli), calculated in diameters, are 7·1–0·8, 19·6–7·1, and so on (Table IV). In the above-mentioned dispersal experiment some flies were recaptured at 2000 yards distance, *i.e.* in the order of ten diameters away. The relative areas are therefore calculated to this distance. To estimate the relative numbers, from a group released at the centre, which would be expected in each annulus from the inverse square relation, the relative areas are each multiplied by $1/D^2$, where $D$ is the distance in units from the centre. For the first annulus, $D$ is 1. A difficulty arises about the population in the central unit, of half-unit radius. Judging by the distribution of recoveries in the traps, the density curve for a released group does not appear to fall off markedly for the first unit zone outwards from the central unit. As a simplifying assumption therefore the density in the central area comprised by the central unit and first adjacent annulus is taken as uniform, *i.e.* the marked population within the central unit itself is one-eighth (0·8/6·3), of that in the first annulus. Their total area (7·1) is therefore multiplied by 1 (= $1/D^2$ for the first annulus), to give the proportion of the marked population in this central zone of one and one-half units diameter. Similarly, the area of the second annulus is multiplied by $1/2^2$, and so on.

TABLE IV

| Radial number of unit | $\pi r^2$ | Relative area of zone | Proportion of population per zone |
|---|---|---|---|
| Central | 0·8 | . | 7·1 |
| 1 | 7·1 | 6·3 | |
| 2 | 19·6 | 13 | 3·3 |
| 3 | 38·6 | 19 | 2·1 |
| 4 | 63·7 | 25 | 1·5 |
| 5 | 94·5 | 31 | 1·2 |
| 6 | 132·7 | 38 | 1 |
| 7 | 176·6 | 44 | 0·9 |
| 8 | 227·1 | 51 | 0·8 |
| 9 | 283·6 | 57 | 0·7 |
| 10 | 346·5 | 63 | 0·6 |
| | | | 19·2 |

Assuming that none of the group has emigrated beyond the outermost annulus, it follows that approximately 7/19, or 37 per cent., of the surviving flies are contained in the central unit and first adjacent annulus. This applies at mid-week if, as assumed, the pattern and degree of dispersal conforms by then to the inverse square relation. This proportion of 7/19 is taken as an average for the decreasing proportion contained in this area during the first week after release.

If the traps are distributed over the whole of a unit of territory, it is obvious that the zone of influence of the traps will extend beyond the territory. The range of attraction is not yet known, but it has been provisionally assumed that the zone of influence from a fully trapped unit of territory extends across the width of the contiguous units with a regularly diminishing influence which ceases at the far border ; it can thus be represented by a zone of full strength influence extending halfway into them—the " equivalent zone of influence ". The fully trapped unit—$100^2\pi$—thus represents only one-quarter of the equivalent zone of influence, the area of which is $200^2\pi$ yards, or approximately 25 acres. The area of the central and first ring of units is $300^2\pi$, *i.e.* the equivalent zone of influence when a unit of territory is being trapped is four-ninths of the combined area of the unit and its surrounding ring of units.

If a group of flies are liberated at a central point, an average of 37 per cent. of the survivors are assumed to be available in that unit of territory or those units immediately adjacent, during the first week. Since the first contour of decreasing density is assumed to lie beyond this first zone of one and a half units from the release point, it follows that four-ninths of 37 per cent., or 16 per cent., are available to traps placed on the release unit of territory.

The overall recovery rate in different experiments with marked blowflies has usually been 4–7 per cent. of the release, the great majority of recaptures usually being taken in the first few days. It follows that something of the order of one-quarter to one-half of the flies actually available for recapture, *i.e.* those which had not died or dispersed beyond the influence of the traps, were taken in these experiments. This seems a reasonable probability, and suggests that the above rather arbitrarily based estimate of availability may not be unduly out.

### (2) *Estimates from Successive Recoveries*

The above factors for mortality and emigration may of course be applied either to serial or single release experiments. To illustrate their use for low-recovery data from serial release experiments, we may again use the data of Table I (*C. erythrocephala* females).

The successive releases may be considered as one experiment, and the estimated total available from all sources used for single day estimates, the principle being analogous to that of Fisher's method and Jackson's negative method, or they may be treated as independent tests, analogous to Jackson's positive, with the mid-week available being calculated instead of the day 0 recovery.

(*a*) *Single day estimates from pooled releases.*—The daily numbers surviving from each release group are calculated in this instance on the basis of 4 per cent. of the original group dying per day (p. 381). From the daily total of these the cumulative recaptures up to the previous day are deducted, giving

TABLE V.—*Data for estimations from pooled recoveries* (*Bracketed figures = recoveries*)

| | Date | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 11.viii | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28.viii |
| | 62 | 60 | 57 | 55 | 52 | 50 | 47 | 45 | 42 | 40 | 37 (1) | 35 | 32 (1) | 30 | 27 | 25 | 22 | 20 |
| | | 23 | 22 | 21 | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 (1) | 12 | 11 | 10 | 9 | 8 | 7 |
| | | | 241 | 231 | 221 (2) | 211 (1) | 201 (3) | 191 | 181 | 171 (2) | 161 (2) | 151 (1) | 141 | 131 (2) | 121 | 111 (2) | 101 (2) | 91 |
| | | | | | | | 220 | 211 (1) | 202 | 193 (7) | 184 (2) | 176 (1) | 165 | 156 (1) | 147 | 138 (2) | 129 (2) | 120 |
| | | | | | | | | | 96 | 92 (2) | 88 (2) | 84 | 80 | 77 (2) | 73 | 69 | 65 | 61 |
| Sum of survivors | | 60 | 79 | 307 | 293 | 280 | 266 | 464 | 441 | 511 | 484 | 459 | 430 | 405 | 378 | 352 | 325 | 299 |
| Less cumulative recaptures | | . | . | . | . | 2 | 3 | 6 | 7 | 7 | 18 | 25 | 28 | 29 | 34 | 34 | 38 | 42 |
| *Free survivors*— | | | | | | | | | | | | | | | | | | |
| Total 1 (all results) | | 60 | 79 | 307 | 293 | 278 | 263 | 458 | 434 | 504 | 466 | 434 | 402 | 376 | 344 | 318 | 287 | 257 |
| Total 2 (first seven days only) | | 60 | 79 | 307 | 293 | 278 | 263 | 458 | 392 | 449 | 254 | 238 | 222 | 270 | 47 | 43 | . | . |
| Total recaptures (1) | | — | — | — | 2 | 1 | 3 | 1 | — | 11 | 7 | 3 | 1 | 5 | — | 4 | 4 | — |
| Total recaptures (2) | | — | — | — | 2 | 1 | 3 | 1 | — | 11 | 4 | 1 | — | 3 | — | — | . | . |
| Samples | | 46 | 314 | 27 | 668 | 167 | 242 | 187 | 142 | 1194 | 816 | 432 | 196 | 577 | 432 | 578 | 936 | 534 |

the total free survivors (Table V). In the table two totals are calculated, the first based on all the data, the second on the results for the first seven days after each release. Ignoring for the moment the tabulation beyond day 7, " pre-estimates " for each day on which there was a recovery may be made from total 2 and the last two rows of the table, irrespective of whether a release was made on that day or not. These pre-estimates are Survivors × Sample/Recaptures. If the average proportion of survivors available during the first week be assumed to represent the proportion available for each day of the week, 16 per cent. of each of these pre-estimates is then the estimate of population density for that day.

(*b*) *Mid-week estimates from single releases.*—As an example, the 13.viii release may be taken. For purposes of illustration the recaptures may be ignored in calculating average survival. The total mortality for the seven days to 20.viii is 7 × 4 per cent. The average available is 16 per cent. of the mean of the survivors at release and seven days later, *i.e.* 16/100 [½(241 + 72/100 of 241)] or 33. The estimate of average density for the week 14–20.viii, *viz.* this " average available " multiplied by the samples for the week, over the recoveries (from 13.viii release only) during the week, is 33 × 2627/8, or, to the nearest hundred, 10,900. This is taken as the estimate for mid-week, *i.e.* 17.viii. The estimates for mid-week 18–24.viii and 20–26.viii are 8900 and 9300.

These three mid-week estimates may be compared with those for the same days by the (*a*) method :

| | 17.viii | 21.viii | 23.viii |
|---|---|---|---|
| (*a*) . . . | 3,400 | 8,300 | 12,600* |
| (*b*) . . . | 10,900 | 8,900 | 9,300 |

* Using full data. No "seven day" recoveries on 23.viii.

Although the agreement for 21.viii is good and 23.viii is reasonable, the wide discrepancy for 17.viii emphasises the unreliability of single day estimates with this type of data.

Obviously, an estimate for a single day by the (*b*) method is only applicable to the mid-week day after a release, unless it be assumed that the calculated " average number available " is sufficiently representative of any individual day in the first week.

As an example of the application of independent mortality and emigration factors to the single-release type of experiment, we may take some data obtained when the population was not in balance, and the analysis will serve incidentally to underline some limitations to the use of these factors. In October, 1953 a single-release experiment, $R/R_3$, was carried out on three " sections ". Details are given in the paper already cited. In this late-season experiment initial and recovery catches were almost entirely *C. erythrocephala*. The initial catch of *L. caesar* for marking was supplemented by laboratory-bred material. Recovery trapping was continued for 38 days, the traps being cleared at two-day intervals. The total post-release catch and total recoveries over the three sections were as follows :

| | Days | | | | |
|---|---|---|---|---|---|
| | 1–8 | 9–16 | 17–24 | 25–38 | Total |
| Total catch . | 33,683 | 16,505 | 8,128 | 1,462 | 59,778 |
| Recoveries . | 226 | 22 | 9 | 0 | 257 |

TABLE VI.—*Some release and recovery data from Single Release Experiment $R/R_3$*

| | Lab. Section | | | Modlin's Section | | | Scrub Section | | |
|---|---|---|---|---|---|---|---|---|---|
| | L.c. | C.e. | Cyn. | L.c. | C.e. | Cyn. | L.c. | C.e. | Cyn. |
| Released (♂/♀) . . | 52/19 | 19/1,083 | –/5 | 75/35 | 8/741 | 1/10 | 62/28 | 25/980 | 1/10 |
| Recoveries 10–12.x . | 1/9 | –/65 | . | 3/12 | –/23 | . | 3/18 | –/48 | –/2 |
| 13–14.x . | . | –/12 | . | . | –/2 | . | . | –/3 | . |
| 17–18.x . | . | –/11 | . | –/1 | –/5 | . | –/1 | –/5 | . |
| Mortality (4% for 8 days) | 17/6 | 6/344 | –/2 | 25/12 | 2/240 | –/3 | 21/9 | 8/312 | –/3 |
| Total deduction . . | 18/15 | 6/421 | –/2 | 28/25 | 2/265 | –/3 | 24/27 | 8/378 | –/5 |
| Surviving at 8 days . | 34/4 | 13/662 | –/3 | 47/10 | 6/476 | 1/7 | 38/– | 17/602 | 1/5 |
| Mean survivors . . | 43/11·5 | 16/873 | –/4 | 61/22·5 | 7/609 | 1/8·5 | 50/14·5 | 21/791 | 1/7·5 |
| Sample 10–12.x . . | 2/63 | 151/4,799 | 2/6 | 4/53 | 238/3,587 | 4/10 | 5/42 | 230/6,103 | 3/17 |
| 13–14.x . . | –/1 | 22/1,358 | –/2 | –/2 | 2/621 | 2/3 | –/1 | 13/400 | 1/4 |
| 15–16.x . . | — | –/57 | –/1 | — | –/14 | 1/– | — | –/18 | — |
| 17–18.x . . | –/24 | 99/5,483 | –/9 | –/17 | 87/3,688 | 1/10 | –/10 | 151/4,163 | –/12 |
| Total . . | 2/88 | 272/11,697 | 2/18 | 4/72 | 327/7,910 | 8/23 | 5/57 | 394/10,684 | 4/33 |
| Total recoveries . | 1/9 | –/88 | — | 3/13 | –/30 | — | 3/19 | –/56 | –/2 |

L.c., *L. caesar*. C.e., *C. erythrocephala*. Cyn., *Cynomyia mortuorum*.

It is clear that little information on density is being lost through confining analysis to the first eight days; the proportion of recoveries to samples is so markedly lower in the second period as to suggest that the released group disappeared very rapidly, either by emigration or through wastage loss in the increasingly unfavourable climatic environment. The details, for *C. erythrocephala*, *L. caesar* and *Cynomyia mortuorum*, are therefore given for the first four trappings only (Table VI). The table illustrates two difficulties which may interfere with the use of loss estimates of the type discussed.

Firstly, the conditions during the experiment must remain reasonably comparable to those under which the loss-rate factors were assessed, otherwise the estimate of mean number available will be misleading. Thus, the mid-week population estimate of female *C. erythrocephala* for the "Lab. section", estimated by the (*b*) method from an "average number available" over the eight days, (16 per cent. of 873) is 18,600. Lincoln index estimates for the second, fourth and eighth day, on the basis of a 4 per cent. (arithmetic) death rate, and assuming 16 per cent. of uncaptured survivors to be available, are 11,800, 15,300 and 56,100 respectively. The last increase almost certainly represents inflation of the estimate by progressive over-estimation of the numbers available, *i.e.* the loss-rate in this experiment probably continued at a very rapid rate after the initial explosive dispersal, this continuing high loss being probably due to mortality rather than to continuing dispersal beyond the trapped zone. The second difficulty is illustrated by the *L. caesar* results. Forty-six of the 48 *L. caesar* (and the only two *Cynomyia*) recovered were taken in the first recovery trapping. Only a straight Lincoln index estimate of their populations, from this first sample alone, would be justified, but the loss-rate, and therefore the estimate of the available marked flies, could only be guessed at.

### (3) *Estimate from Pooled Results*

Estimates for single days, even over several releases—the (*a*) method—will often be impossible where the recovery rate is low; in our serial release experiments the method provided very few reliable estimates for other sets of data than that of Table I. Some method of averaging the individual day estimates is required, even though this must blanket day-to-day fluctuations. Where *nil* recoveries are infrequent, this could be achieved by taking a mean of the estimates weighted for numbers of recoveries. Since samples of reasonable size in which there are no recoveries must have significance, the convention could be adopted of assuming that the next fly to be caught would have been a marked fly, *i.e.* recovery is 1 for $n + 1$. This, however, would obviously overstate the recovery rate if many of the recoveries were a single fly, as frequently happens with the less numerous species, and it is probably preferable to combine the sample for a *nil*-recovery day with that for the adjacent day, as suggested by Fisher and Ford (*loc. cit.*).

A weighted mean estimate would obviously be unsuitable except for data where *nil*-recovery days were rare. For estimating from the $R/R_1$ and $R/R_2$ serial release experiments (MacLeod and Donnelly, 1957*a*) the method actually used was a combination of the (*a*) and (*b*) methods outlined above. It is admittedly an over-simplification, but is at least applicable to all the sets of data in these experiments. The data of Table I will again serve to illustrate its use. The daily free survivors are totalled as for the (*a*) method, for the

duration of the experiment (totals 1 or 2 of Table V). From this an " average-of-survivors " value for the period is then obtained ; 16 per cent. of this value estimates the mean number available in the trapping zone over the trapping period. The rest of the calculation is as for method (*b*) ; the appropriate totals of samples and recoveries, and the estimated mean available number are used for an " estimate-from-pooled results " for the population, *viz.* $\hat{P}$ = Estimated mean available × Total samples/Total recoveries.

The full period, instead of the first seven days, may be used so as to incorporate all the recovery information in Table V. The estimate, and for comparison that for the seven-day part of Table V (based on totals 2 of availables and recaptures, and using the total samples up to 26.viii only), are :

| | Mean of survivors | Mean available | Total recoveries | Total samples | Estimate |
|---|---|---|---|---|---|
| Full data | 327 | 52 | 42 | 7488 | 9300 |
| Seven days | 240 | 38 | 26 | 6018 | 8800 |

Evidence of inflation, from over-estimating the numbers available over the full period, is negligible in this case, and it may well be that the 16 per cent. factor, in this test, was still reasonably appropriate for measuring availability even after the first week.

### (4) *The Confidence of the Estimate*

The approximations and simplifications used for the above population estimates from pooled releases and recoveries are too sweeping for any simple variance estimate to be applicable. The experimental conditions and the experimenter's knowledge of the background of the problem can help to keep minimal the bias introduced, for example, by the averaging of total and/or available survivors, and by using independently obtained estimates of rate of change of the population. As pointed out earlier, the problem, irrespective of which method of analysis is used, is essentially one of determining the population from three terms, the marked insects available for capture, the number of marked and the total number in the sample. In the simplified method for low incidence recoveries, the reliability of the estimate of the first term depends on knowledge of the ecology of the insect concerned, and of the impress of, for example, the weather and topographic conditions of the particular experiment. The remaining two terms form a ratio which will be affected both by random error in sampling and by the bias due to the pooling of successive samples taken in a range of time over which the availables have been averaged but in which the size of the catches may not necessarily have been uniformly distributed. This latter source of error is, in fact, inherent in any of the methods where there is an appreciable lapse of time during sampling. It cannot readily be allowed for, but under reasonably uniform weather conditions, and assuming absence of systematic sources of error, the effect may be ignored, and the total samples and recoveries over the period treated as single values for unit time. The probable magnitude of random error to be anticipated in the final estimate of numbers should then be indicated by the range of probable error of the observed ratio.

For an estimate of population density based on the straightforward Lincoln index, *i.e.* in the exceptional case where the unadjusted values for marked releases sample and recoveries may be used directly, Bailey gives the variance as (approximately) $V = M^2(S + 1)(S - R)/(R + 1)^2(R + 2)$. It will occasionally be possible to use this for isolated sets of results in a serial release experiment, or for, say, the first recovery of a serial recovery experiment.

Where one is limited to estimating the error of an observed recapture ratio, as in the estimate from pooled results, a snap estimate of the order of error range to be expected may be made very simply by taking the square root of the recapture number as an approximation to its standard deviation. This rule of thumb method, suggested by Ricker (1948), is based on the fact that in a population of which a proportion $p$ is marked, if the marked and unmarked are representatively sampled, then $R = Sp$. Now $R$ is a sample from the Binomial distribution of possible recoveries, of which the mean is also $Sp$. The variance of $R$ is therefore the variance of the Binomial mean, which is $Sp(1 - p)$. The smaller the ratio $p$, the closer the variance approximates to $Sp$, which should equal $R$, *i.e.* the closer the standard deviation of $R$ approaches to its square root.

With very low absolute values of $R$, the probable range of random error, *i.e.* the confidence interval, is so unequally divided above and below the observed value that an estimate of standard deviation is not directly applicable for assessing the limits of the interval, and it is better to use the published tables of confidence intervals for the Binomial. These give the limits above and below the sample value within which the odds are known that the true value will lie. Provided the sampling is random an estimate can always be made in this way of the reliability of an observed recapture ratio, which will at least indicate the order of magnitude of the sampling error to be accepted in the final estimate of population. The confidence intervals for the Binomial are given by Clopper and Pearson (1934), Fisher and Yates (1948), and in other statistical text-books. Adams (1951) has published charts for reading off directly the confidence limits for the Poisson distribution, as well as the Clopper and Pearson charts. The former are useful particularly when the recoveries are relatively few in the sample.

It must be borne in mind that if the distribution of the samples is not random, then all these estimates of sampling error will be too conservative. If there is reason to believe that any such disturbance of the random is present, allowance should be made for this in the assessment of the range of sampling error. Non-random distribution of samples might arise, for instance, from a tendency to aggregation of individuals in either the marked or the unmarked population, or again from a tendency for unnatural concentrations, such as trap catches, to be attractive to untrapped individuals which would otherwise remain randomly distributed.

## VI. Discussion

There is at present no practicable method of assessing the absolute density of mobile insect populations other than by use of the Lincoln index principle. There are theoretical and practical objections which can be raised to this method. The principal theoretical one is that heterogeneous populations can

be accurately estimated only if they are representatively sampled either for marking or for recovery; otherwise each component must be estimated separately. Significant heterogeneity may lie in unmeasurable or undetected differences, and the components themselves may not be always recognisable. The main practical objections relate to the difficulty of determining the rate of change in numbers of marked insects available required since there must be a time lag between release and recovery. With blowflies, and probably with many other mobile organisms, a fixed rate is inapplicable, since loss-rate apparently consists of a more or less regular mortality rate plus an explosive initial spread from the release point followed by a slower emigration rate out of the area.

Further experimentation may yield improved estimates of these two sources of loss of material available to sampling, but it is doubtful if a generalisation can justifiably be made for either loss. The wastage fraction of the mortality will almost certainly vary widely according to the environmental circumstances of the occasion, and the emigration rate similarly will in all probability depend on both climatic and edaphic conditions.

A partial solution to the dispersal problem would be to avoid an initial concentration by releasing from numerous distributed foci over an area greater than the zone of influence of the group of recovery traps, in which case only the second part of the dispersal loss—the emigration rate—would require to be assessed.

A practical difficulty lies in the marking of adequate numbers of local specimens of the less frequent species or components of the population, and without large open-air insectaries it is not possible to produce comparable non-native samples.

Where an estimate can be made by a simple Lincoln index test involving one release and one recapture, under conditions where the interval is so short that the degree of population change in the interim may be considered negligible, then the reliability of the estimate, for a single component, is largely dependent on the size of the sample and the proportion of recoveries. In such case the confidence limits for the estimate are probably reasonably well approximated by those for the ratio of recoveries to sample, which will in the usual case be equivalent to the limits for a Poisson distribution.

With the type of data discussed in the present paper, the simple Lincoln index will seldom be applicable. Low or *nil* recoveries, with the consequent need for repetitive recovery sampling, will generally compel the use of some modification of the basic formula to include an assessment of loss-rate of marked specimens. It would appear that, at least in so far as blowflies are concerned, so many assumptions must be made for this assessment that attempts at precise estimation of numbers are at present unjustified. Nevertheless, information of qualitative value can be obtained by the release-recapture method even in its present inefficient form. Provided it be accepted that the confidence limits for any estimate of insect numbers involving a loss-rate assessment are probably wide, and that at present there is not enough evidence for erecting a physical or stochastic model from which these limits could be derived, provisional quantitative inferences of absolute numbers may reasonably be drawn from the results and compared with observed relative numbers.

In the present paper, a method of pooling the information from the first

week's recoveries is suggested by which some sort of estimate may be extracted even from low-frequency recoveries. With rather higher frequency of recoveries the averaging may be confined to the estimation of the numbers available, and separate estimates may be made for individual days. An additional bias is, however, introduced in this case, particularly for the first and possibly the second day, when the initial very rapid dispersal from the release focus may not have given way to the subsequent apparently random movements producing a steady loss by emigration out of the area. The method has at least this in its favour—that further information gained by experiments on dispersal may be applied directly to improving the precision of estimates without changing the essential form of the analysis method.

## VII. Summary

The three major approaches to the analysis of data from multiple releases and recaptures which are applicable to experiments with insects are described, *viz.* Fisher's method, Jackson's early and later methods, and Bailey's triple-catch method. The common relationship of the three to the Lincoln index is examined.

Some difficulties in applying the release-recapture technique to the estimation of numbers of mixed populations of mobile insects are outlined.

None of the three analysis methods is suitable for interpreting release-recapture data in cases where (*a*) the loss-rate of marked insects over a subsequent run of time-intervals cannot be represented by a constant factor, and (*b*) the incidence of recaptures is generally low, with many blank days. The weaknesses of the three analysis methods under these circumstances are illustrated by an example of their application to a set of blowfly data.

In work on wild blowfly populations it was found that, because of the difficulty of fully identifying all the species in samples when these are required to be released subsequently, a single release was preferable to serial releases, subsequent serial samples being retained for identification. Information on loss-rate, normally supplied by successive releases, was more satisfactorily obtained by independent experiments, since it did not appear to be a regular rate.

Simple methods, evolved for blowfly studies, are described for pooling results from single or serial releases where the recoveries are poor, so as to extract an estimate of numbers. In these the mortality is estimated from laboratory controls; the emigration rate beyond the zone of influence of the traps is calculated from independent experiments on dispersal rate of a concentration of marked flies.

## VIII. References

Adams, L., 1951, Confidence limits for the Petersen or Lincoln index used in animal population studies. *J. Wildlife Mgmt.* **15** : 13.19.

Bailey, N. T. J., 1951, On estimating the size of mobile populations from recapture data. *Biometrika* **38** : 293–306.

—— 1952, Improvements in the interpretation of recapture data. *J. Anim. Ecol.* **21** : 120–7.

Clopper, C. J. and Pearson, E. S., 1934, The use of confidence or fiducial limits applied to the use of the Binomial. *Biometrika* **26** : 404–13.

Cragg, J. B. and Hobart, J., 1955, A study of a field population of the blowflies *Lucilia caesar* (L.) and *L. sericata* (Mg.). *Ann. appl. Biol.* **43** : 645–63.

Craig, C. C., 1953, On the utilization of marked specimens in estimating populations of flying insects. *Biometrika* **40** : 170–6.

Dowdeswell, W. H., Fisher, R. A. and Ford, E. B., 1940, The quantitative study of populations in the Lepidoptera. 1. *Polyommatus icarus* Rott. *Ann. Eugen., Camb.* **10** : 123–6.

—— —— —— 1949, The quantitative study of populations in the Lepidoptera. 2. *Maniola jurtina* L. *Heredity* **3** : 67–84.

Fisher, R. A. and Ford, E. B., 1947, The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* L. *Ibid.* **1** : 143–74.

—— and Yates, F., 1948, *Statistical Tables.* 3rd Ed. London.

Gilmour, D., Waterhouse, D. F. and McIntyre, G. A., 1946, An account of experiments undertaken to determine the natural population density of the sheep blowfly, *Lucilia cuprina* Wied. *Bull. Coun. sci. indust. Res. Aust.* No. **195** (39 pp.).

Hammersley, J. M., 1953, Capture-recapture analysis. *Biometrika* **40** : 265–**195** 78.

Jackson, C. H. N., 1933, On the true density of tsetse flies. *J. Anim. Ecol.* **2** : 204–9.

—— 1937, Some new methods in the study of *Glossina morsitans*. *Proc. zool. Soc. Lond.* **1936** : 811–96.

—— 1939, The analysis of an animal population. *J. Anim. Ecol.* **8** : 238–46.

—— 1940, The analysis of a tsetse-fly population. *Ann. Eugen., Camb.* **10** : 332–69.

—— 1944, The analysis of a tsetse-fly population. II. *Ibid.* **12** : 176–205.

—— 1946, An artificially isolated generation of tsetse flies (Diptera). *Bull. ent. Res.* **37** : 291–9.

—— 1948, The analysis of a tsetse-fly population. III. *Ann. Eugen., Camb.* **14** : 91–108.

Leslie, P. H. and Chitty, D., 1951, The estimation of population parameters from data obtained by means of the capture-recapture method. I. The maximum likelihood equations for estimating the death rate. *Biometrika* **38** : 269–92.

Lincoln, F. C., 1930, Calculating waterfowl abundance on the basis of banding returns. *Circ. U.S. Dep. Agric.* **118**.

MacLeod, J. and Donnelly, J., 1956, Methods for the study of blowfly populations. II. The use of laboratory-bred material. *Ann. appl. Biol.* **44** : 643–8.

—— —— 1957*a*, Some ecological relationships of natural populations of Calliphorine blowflies. *J. Anim. Ecol.* **26** : 135–70.

—— —— 1957*b*, Individual and group marking methods for fly population studies. *Bull. ent. Res.* **48** : 585–92.

Richards, O. W., 1953, The study of the numbers of the Red Locust, *Nomadacris septemfasciata* (Serville). *Anti-Locust Bull.* **15**. London. Brit. Mus. (Nat. Hist.) (30 pp.).

—— and Waloff, N., 1954, Studies on the biology and population dynamics of British grasshoppers. *Ibid.* **17**. London. Brit. Mus. (Nat. Hist.) (182 pp.).

Ricker, W. E., 1948, Methods of estimating vital statistics of fish populations. *Ind. Univ. Publ.* (*Sci.*) **15** : 1–101.